

# STUDIES IN THE PIGMENTARY SYSTEM OF CRUSTACEA

## II. DIURNAL MOVEMENTS OF THE RETINAL PIGMENTS OF BERMUDAN DECAPODS

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Diurnal rhythms in behavior and physiological rhythms in certain organ systems of animals have long intrigued biologists and led to much interesting speculation as to the nature of the mechanisms involved in such activities. That the phenomenon is a general one is seen from the cases cited by Welsh (1930a). Such periodicity is most strikingly exhibited in the pigmentary changes of various animals, being reported in shrimps by Gamble and Keeble (1900), in brachyurans by Megušar (1912), in isopods by Menke (1911), in amphibians by Slome and Hogben (1929), in reptiles by Redfield (1918), and in cyclostomes by Young (1935). It is reasonable to expect that further study will reveal the existence of such rhythms in additional forms. Welsh (1930a, 1935, 1936) has shown that diurnal changes in the migration of the retinal pigments occur in several crustaceans even though the animals are maintained under constant conditions of illumination or of darkness.

In all the cases mentioned hormonal factors are involved to a greater or lesser degree in controlling pigmentary activity. Since the present studies (Kleinholz, 1937) are concerned with chromatic responses in crustaceans, only this branch of the general subject of color changes will be discussed here. The control of the bodily changes in color in crustaceans has been shown by Perkins (1928) and by Koller (1928) to be maintained by an endocrine which is liberated into the circulatory system from within the eye-stalks. Hanström (1935) and his associates (Sjögren, 1934; Carlson, 1936) have made histological studies of the eyes of many crustaceans, and have correlated the activity of the chromatophorotropic principle in eye-stalk extracts with the presence within the eye-stalk of a secretory structure which they call the *blood gland*. The mechanism that is involved in the control of retinal pig-

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ment migration in crustaceans is not yet completely known. Recent studies on *Palæmonetes vulgaris* (Kleinholz, 1936) present evidence for a humoral control of the distal and the reflecting pigments in the retina, but the proximal pigment appears not to be affected by the same eye-stalk extracts which activate the first two sets of pigments. It is possible that one set of pigment cells is under nervous and the others under hormonal control.

Before much progress can be made in analyzing the mechanisms by which diurnal rhythms are maintained under constant external conditions, it is advisable to study the phenomenon in a number of different species to determine which combinations of retinal pigments may be involved in such activities. This report on diurnal changes in the retinal pigments of several Bermudan crustaceans is offered to this end.

#### MATERIALS AND METHODS

The various crustaceans used in these experiments were obtained by dredging at several stations in the vicinity of the Biological Station. After a sufficient number of animals of the same species had been brought into the laboratory, the specimens were divided into two groups, one of which was placed in a white porcelain bowl illuminated by a 40-watt electric lamp at a distance of 18 inches, while the second group was placed in a container in the dark-room. At least 12 hours were allowed for individuals to become adapted to light and to darkness.

After a period appropriate for adaptation, specimens were removed for fixation of the retinal pigments. For purposes of description the term "day-light" eye is used to indicate the retina of a specimen that was kept constantly illuminated and which was fixed or examined in the daytime, while "night-light" eye represents the condition of the pigments in an illuminated retina that was fixed at night; conversely, "day-dark" and "night-dark" are used to designate those specimens maintained in constant darkness whose retinal pigments were fixed during the day and at night, respectively. When a specimen was taken from the light-adapted group, a similar specimen was removed from the container in the dark-room for fixation at the same time.

Two methods of fixation for histological study were used. In one method, the animals were dropped into hot water (80° C.) for 10-20 seconds to fix the positions of the retinal pigments, and were then transferred either to 5 per cent formalin or to a modified Bouin's solution containing 7 per cent acetic acid. In the second method the entire specimen, after the usual period of adaptation to darkness or to light, was dropped into a vial of Bouin's solution. The exoskeleton of most of the crustaceans contained large amounts of calcareous salts, but these

troublesome deposits were dissolved by the acetic acid in the fixative, so that sectioning the eyes was greatly facilitated.

When the exoskeleton had been sufficiently softened by the fixative, the eye-stalks were excised and embedded in paraffin by a rapid dioxane treatment. After a preliminary rinsing of the excised eyes in water, the stalks were rolled over filter paper to remove any excess moisture

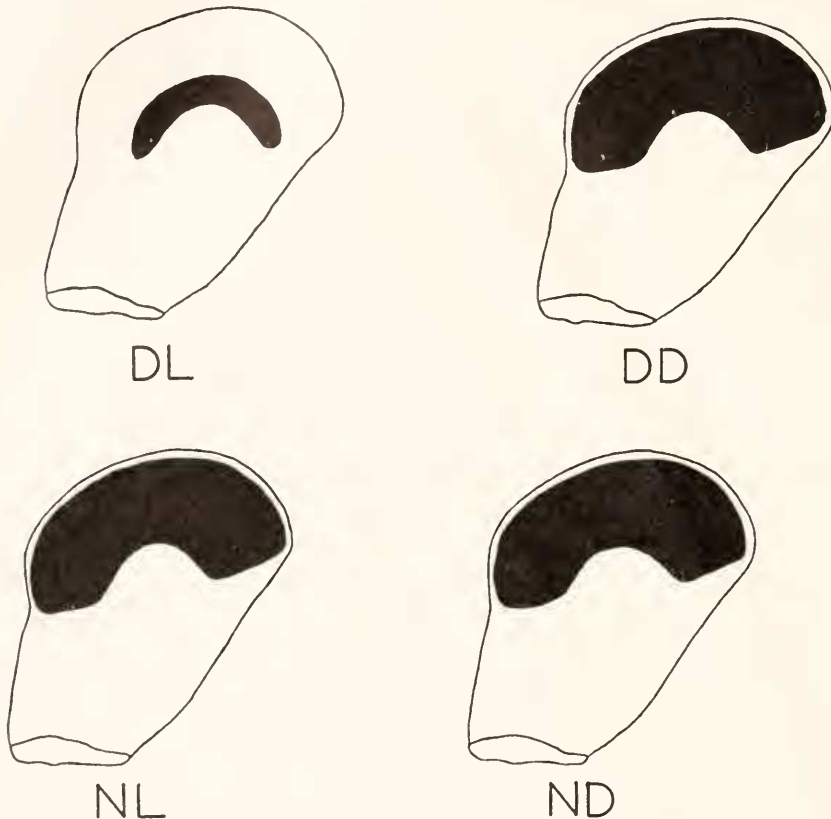


FIG. 1. Entire eye-stalks of *Eusicyonia*, viewed by transmitted light through the low powers of the microscope and showing the positions of the distal retinal pigment. *DL*, from a day-light animal; *DD*, from a day-dark specimen; *NL*, from a night-light individual; *ND*, from a night-dark shrimp.

and were then placed in full-strength dioxane over anhydrous calcium chloride. They were left in this fluid usually overnight (8-10 hours) and the next morning were placed directly into soft paraffin. The tissues were allowed to become infiltrated with the wax for about three hours, using two changes of paraffin, and were then embedded. No difficulty was encountered in cutting serial sections at 10 micra. Some

sections were subsequently stained with Delafield's hematoxylin and eosin, and others were mounted unstained.

I am indebted to Mr. M. D. Burkenroad of the Bingham Oceanographic Foundation at Yale University, and to Dr. Fenner Chace, Jr., of the Museum of Comparative Zoölogy at Harvard University for identifications of the collected crustaceans. The two macrurans studied were *Eusicyonia n. sp.* (to be described by Mr. Burkenroad) and *Trachypencopsis mobilispinis*, while the brachyurans were *Portunus anceps*, *Portunus depressifrons*, *Parthenope serrata*, and *Calappa flammea*.

*Eusicyonia n. sp.*

This new species of shrimp was taken from dredgings at 10-15 fathoms off Murray's Anchorage. Of the 12 specimens obtained for experimental study, 2 were males and the rest females.

While preliminary observations of the eyes of specimens kept under constant illumination showed that there was a change in position of the distal retinal pigment at night (Fig. 1), sectioning the eye was necessary to disclose the photomechanical changes of the remaining pigments. The eye of *Eusicyonia* is similar in structure to that of *Palæmonetes* as described by Parker (1897) and by Welsh (1930*b*). The positions of the three types of pigment cells are shown in Figs. 2-5.

An unusual situation was discovered in studying a number of sectioned eye-stalks of this species. Of the 12 specimens at hand, the retinas of 4 showed complete absence of reflecting pigment. The possibility that this might be a secondary sexual difference is eliminated by the fact that 2 of these shrimps were males and 2 females. The possibility that the difference is a fixation artifact can be ruled out by comparing eyes of specimens fixed by the two different methods. The reflecting pigment in the integument of many of the lower vertebrates is guanine, and is commonly found there in the crystalline condition (Ewald and Krukenberg, 1882). So far as I know, however, no studies have been made on the chemical nature of the pigments in the crustacean retina. If the retinal reflecting pigment is guanine, it might be slightly soluble in the acid components of the Bouin's solution. But the pigment was lacking only from those eyes which had been fixed with hot water and then preserved in formalin. This treatment does not seem to be sufficiently harsh to effect such changes. Moreover, of 4 specimens of *Trachypencopsis* which had been fixed by the same method, the eyes of 1 lacked this reflecting pigment, while those of a second specimen were slightly deficient (Fig. 15); the retinas of the other 2 animals showed what may be called "typical" amounts. It seems more likely that the differences in amount of reflecting pigment are due to

individual variations, possibly in the nucleoprotein metabolism of the animals, than to any fixation artifact.

On studying sections of the eyes of *Eusicyonia* fixed under the four experimental conditions (Figs. 2-5, 10-13) the following situation is found in the retinal pigments. The granules of reflecting pigment undergo no apparent changes in position in response to changes in light intensity. The main mass of the reflecting pigment is located on the distal face of the basement membrane; smaller amounts are found below the basement membrane and capping the distal ends of the distal retinal cells. The distal and the proximal pigments show readily discernible photomechanical changes:

Day-light eye

- A. The distal pigment cells are to be found in the typical light-adapted state, the cells having moved proximally and come to rest against the proximal reticular cells.
- B. The proximal pigment is also in the position typical for the light-adapted retina, much of it having migrated above the basement membrane to surround the rhabdome.

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EXPLANATION FOR PLATE I

All figures are camera-lucida outlines to insure correct proportions, but the details have been drawn diagrammatically. *BM*, basement membrane; *DD*, day-dark retina; *DL*, day-light retina; *DP*, distal retinal pigment; *ND*, night-dark eye; *NL*, night-light retina; *PP*, proximal retinal pigment; *RP*, reflecting retinal pigment; *R*, rhabdome.

FIG. 2. Ommatidium from a day-light eye of *Eusicyonia*. The distal pigment lies against the proximal reticular cells, while much of the proximal pigment has migrated above the basement membrane to surround the rhabdome.

FIG. 3. Ommatidium from a day-dark retina of *Eusicyonia*. The pigments are in the typical dark-adapted position, the distal pigment having migrated distally towards the cornea, and the proximal pigment having moved completely below the basement membrane.

FIG. 4. Ommatidium from a night-light eye of *Eusicyonia*. The distal pigment is in the position characteristic for the dark-adapted retina while the proximal pigment is found above the basement membrane.

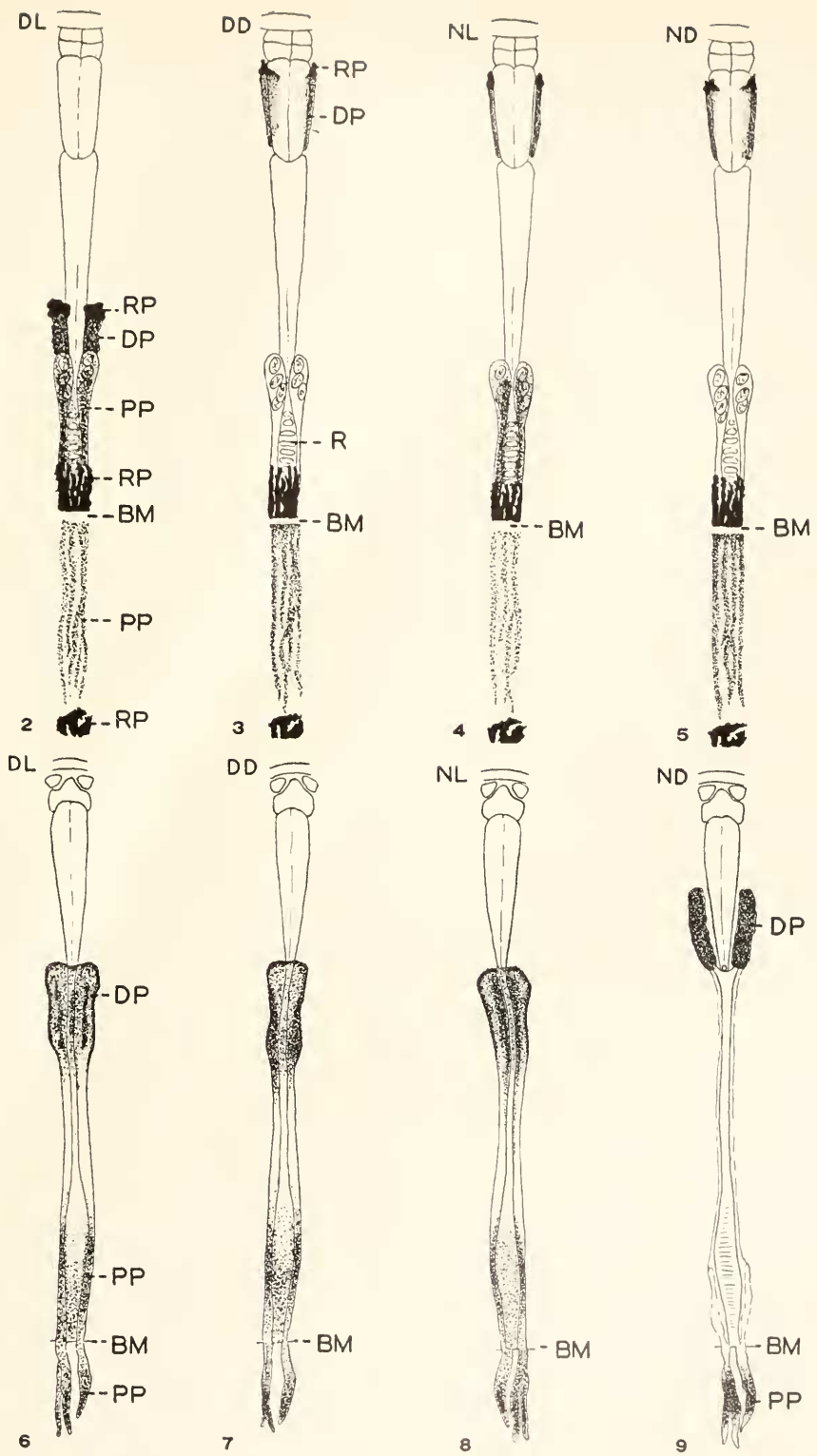
FIG. 5. Ommatidium from a night-dark eye. Both pigments are in the positions expected for a dark-adapted retina.

FIG. 6. Ommatidium from a day-light eye of *Portunus anceps*. The distal pigment is dispersed proximally toward the basement membrane, while much of the proximal pigment has migrated distally above the basement membrane.

FIG. 7. Ommatidium from a day-dark retina of *Portunus*. The positions of the pigments are the same as in the day-light eye, in spite of the fact that the animals were kept in constant darkness.

FIG. 8. Ommatidium from a night-light eye of *Portunus*. The positions of the retinal pigments are typical for what is expected in an illuminated eye.

FIG. 9. Ommatidium from a night-dark eye of the same species. The distal pigment has migrated distally, while the proximal pigment has moved proximally below the basement membrane.



## Day-dark eye

- A. The distal pigment is in the position characteristic for the dark-adapted retina, forming a collar around the distal ends of the cones.  
 B. The proximal pigment has moved entirely below the basement membrane.

## Night-light eye

- A. The distal pigment, in spite of the fact that the retina has been under constant illumination, is in the position typical for the dark-adapted eye, at the distal ends of the cones.  
 B. The proximal pigment, however, is in the position found in the usual light-adapted eye, much of it having moved above the basement membrane.

## Night-dark eye

- A. The distal pigment is in the position characteristic for a dark-adapted retina.  
 B. The proximal pigment is also in the position found in the dark-adapted eye, having migrated completely below the basement membrane.

## EXPLANATION OF PLATE II

Figs. 10-13 represent retinas of *Eusicyonia* in the four experimental conditions; Figs. 14-17 are photographs of similar retinas of *Trachypencopsis mobilispinis*; Figs. 18-21 are photographs of the entire stalks of *Portunus anceps*. All the eyes are oriented so that the distal end of the retina is at the left and the proximal end to the right. *D*, distal pigment; *P*, proximal pigment; *R*, reflecting pigment.

FIG. 10. Day-light retina. The distal pigment has migrated proximally, the proximal pigment has moved above the basement membrane and lies directly to the right of the distal pigment, but the reflecting pigment is fixed.

FIG. 11. Day-dark retina. The distal pigment is seen to the left in its distal position, while the proximal pigment has migrated completely below the basement membrane.

FIG. 12. Night-light retina. The distal pigment is in the same position as in the day-dark retina, but the proximal pigment (which has been retouched in this photograph) is in the typical light-adapted position.

FIG. 13. Night-dark retina. The distal and the proximal pigments are in the positions characteristic for a dark-adapted eye.

Figs. 14-17 are comparable retinas of *Trachypencopsis*, arranged in the same sequence as Figs. 10-13 and showing similar movements of the retinal pigments. Fig. 15 shows the very small amount of reflecting pigment in this retina compared with the others of this series.

FIG. 18. Day-light eye of *Portunus*. The distal pigment is the black band to the left. Granules of this pigment are dispersed proximally, while granules of the proximal pigment are dispersed distally towards the left.

FIG. 19. Day-dark eye. The positions of the two pigments are the same as in Fig. 18, in spite of the fact that the animals were maintained in constant darkness.

FIG. 20. Night-light eye. The pigments are in the positions characteristic for a light-adapted retina.

FIG. 21. Night-dark eye. The granules of the distal pigment have migrated distally from the processes in which they had been dispersed, while the proximal pigment granules have moved completely below the basement membrane. The blackness of the processes is due to the stain, and not to any contained pigment.

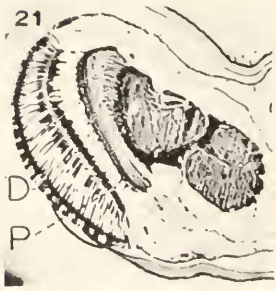
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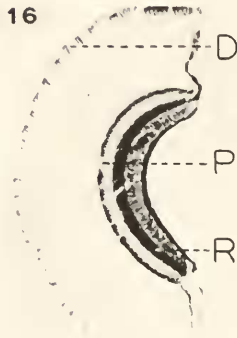
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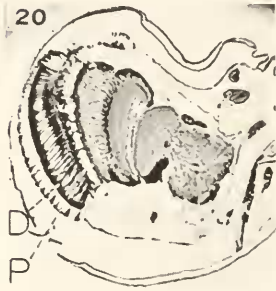
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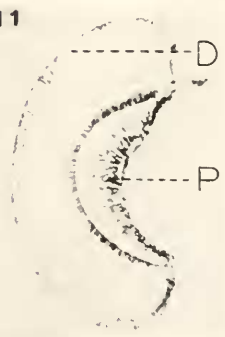
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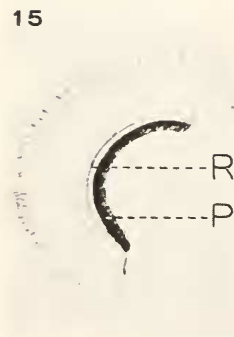
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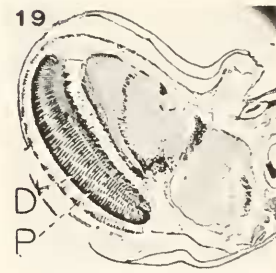
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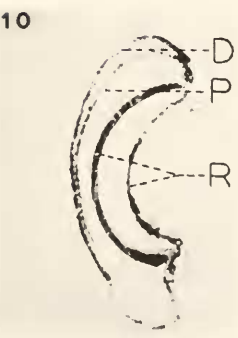
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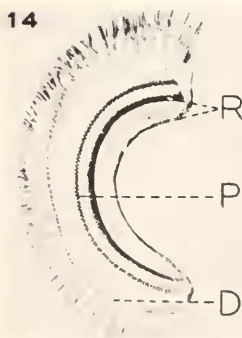
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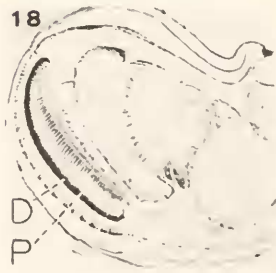
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*Trachypencopsis mobilisfinis*

Crustaceans of this species were dredged off sandy bottoms in Castle Harbor and in Bailey's Bay. Eight animals were available for study; three of these were males and the rest females.

A particularly thick exoskeleton and dense pigmentation obscured the eye-stalk so that the positions of the distal retinal cells of whole eyes could not be determined by direct microscopic examination. Study of sectioned retinas, however, revealed a close similarity to the condition found in *Eusicyonia*, the chief difference being in the size relationships of the ommatidial components.

In this species, too, the reflecting pigment apparently undergoes no positional changes. In some specimens this pigment was completely absent, and in one only a trace of it was evident (Fig. 15). The retinal responses to light and to darkness are so similar to those in *Eusicyonia* that the same diagrams of Plate I (Figs. 2-5) serve to illustrate the changes. The distal and the proximal pigments show the usual positional changes in adaptation to light and to darkness. The resemblance to *Eusicyonia* in this respect is heightened by the fact that the persistent diurnal rhythm is found in the distal pigment cells, which, in night-light eyes, are in the position characteristic for a dark-adapted retina.

*Brachyurans*

Four species of brachyuran crustaceans were studied for the movements of the retinal pigments. Since the responses in all four were found to be identical, they may conveniently be described together.

## EXPLANATION OF PLATE III

Figs. 22-25 are retinas of *Parthenope serrata* and Figs. 26-29 represent those of *Calappa flammaea*. The retinas are oriented with the distal end at the top of the photograph and the proximal end toward the bottom. *D*, distal pigment; *P*, proximal pigment.

FIG. 22. Day-light retina. The distal pigment is dispersed proximally while the proximal pigment granules have migrated, for the most part, above the basement membrane.

FIG. 23. Day-dark retina. The positions of the two pigments are the same as in the day-light eye, in spite of constant darkness.

FIG. 24. Night-light retina. The pigments are in the positions typical for the light-adapted eye.

FIG. 25. Night-dark retina. The granules of the distal pigment have retreated distally, while those of the proximal pigment have withdrawn completely from the processes to a position below the basement membrane.

Figs. 26-29 are photographs of retinas of *Calappa* arranged in the same sequence as Figs. 22-25 and showing a similar persistent rhythm in the day-dark eye.

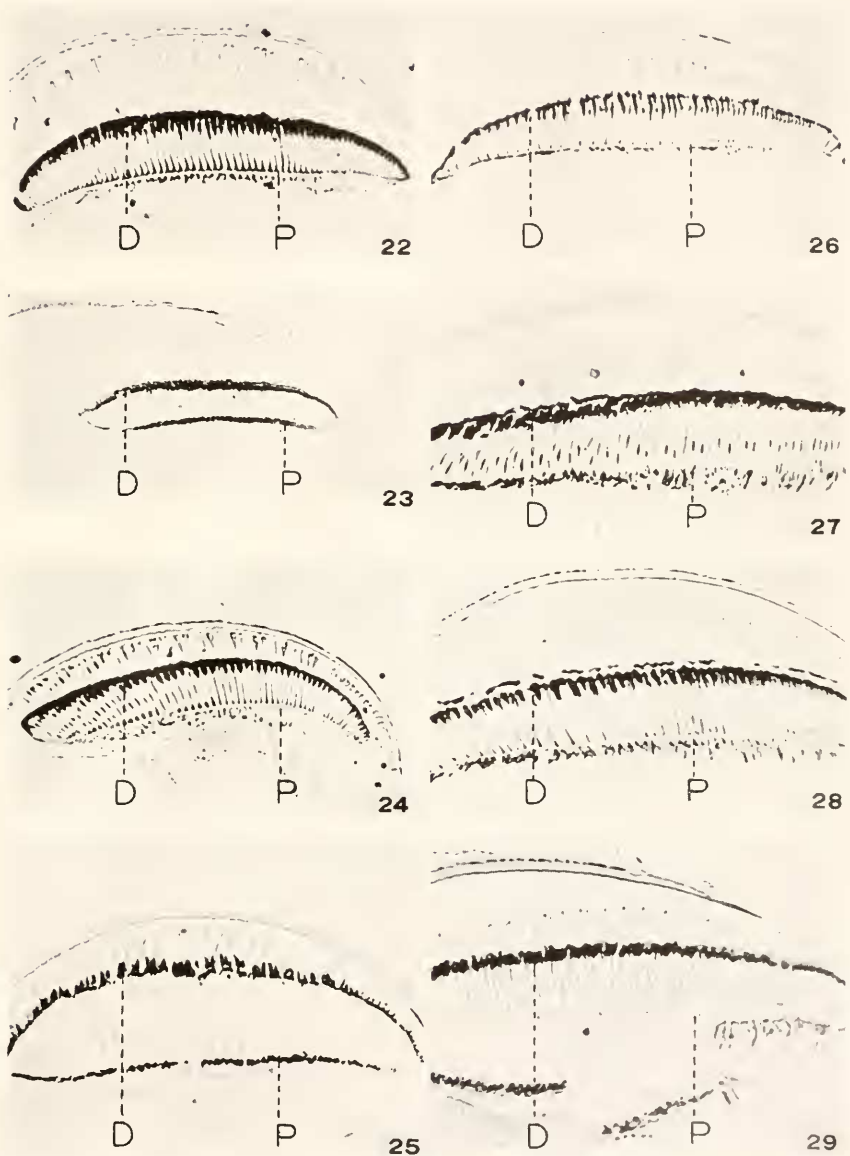


PLATE III

There are two types of black retinal pigments in these animals, a proximal and a distal set of cells: reflecting pigments seem to be completely absent. Diagrammatic illustrations of ommatidia are shown in Figs. 6-9.

The photomechanical changes of the retinal pigments in these brachyurans, although not as marked as those in the macrurans, are still evident:

Day-light eye

- A.* The distal pigment is dispersed proximally toward the basement membrane.
- B.* Most of the proximal pigment has migrated above the basement membrane and surrounds the rhabdome.

Day-dark eye

- A.* The distal pigment remains in the position typical for a light-adapted retina.
- B.* The proximal pigment also shows the persistent rhythm, remaining in the position found in a light-adapted eye in spite of conditions of constant darkness.

Night-light eye

- A.* The distal pigment granules are in the same position as in the day-light eye.
- B.* The proximal pigment is also in the light-adapted position.

Night-dark eye

- A.* The distal pigment granules have retreated distally from the processes and lie in the cells which are located along the posterior region of the cones.
- B.* The proximal pigment has moved completely below the basement membrane so that the processes of these cells are entirely free of pigment granules.

### DISCUSSION

There is still much ignorance as to the nature of the mechanisms involved in these rhythmic activities. If the retinal pigments were uniform in their periodic responses under constant conditions, the problem as to the mediating agents would be relatively simple. But published accounts of the behavior of these pigments among the different crustaceans reveal perplexing heterogeneities in this respect. Examination of Table I will show the responses reported for various crustaceans.

In the first four species of macrurans, there is a uniformity of response in that the same set of retinal pigment, the distal, shows persistent periodic movements in the same direction under the same conditions of illumination. The next two species of shrimps are unusual in that they show evidence of possessing a double rhythm; not only are distal and reflecting retinal pigments involved in the periodic migration, but the periodicity occurs twice within a 24-hour cycle, once during the daytime when the animals are maintained in darkness, and once at night when the shrimps are kept under constant illumination.

Up to this point, the various responses, although still slightly confusing, are open to interpretation on a hormonal basis as found in the case of *Palaeomonetes* (Kleinholz, 1936). The puzzling situations are those where the distal pigments show a persistent rhythm, but the reflecting pigments at the same time undergo only the normal changes in position characteristic for the particular condition of illumination. In *Leander tenuicornis* and in *Latreutes fucorum* the situation is reversed, the reflecting pigments showing the rhythm while the distal pigment cells respond only to differences in light intensity. If endocrine control of these two pigments is universally present in the crustaceans,

TABLE I

Crustacean	Distal	Reflecting	Proximal	Investigator
<i>Macrobrachium olfersii</i> . . . . .	NL	—	—	Welsh (1930a)
<i>Macrobrachium acanthurus</i> . . . . .	NL	—	—	Welsh (1930a)
<i>Eusicyonia</i> n. sp. . . . .	NL	Ab. or F	—	This paper
<i>Trachypeneopsis mobilispinus</i> . . . . .	NL	Ab. or F	—	This paper
<i>Leander affinis</i> . . . . .	DD and NL	DD and NL	—	Welsh (1935)
<i>Anchistioides antiguensis</i> . . . . .	DD and NL	DD and NL	—	Welsh (1936)
<i>Portunus anceps</i> . . . . .	DD	Ab.	DD	This paper
<i>Portunus depressifrons</i> . . . . .	DD	Ab.	DD	This paper
<i>Parthenope serrata</i> . . . . .	DD	Ab.	DD	This paper
<i>Calappa flammea</i> . . . . .	DD	Ab.	DD	This paper
<i>Leander tenuicornis</i> . . . . .	—	NL	—	Welsh (1935)
<i>Latreutes fucorum</i> . . . . .	—	NL	NL	Welsh (1935)
<i>Cambarus virilis</i> . . . . .	—	—	DD	Bennitt (1932a)
<i>Peneopsis goodei</i> . . . . .	F	F	DD	Welsh (1935)

—, pigment shows normal photomechanical changes but shows no periodicity.

Ab., pigment is absent from the retina.

F, pigment is present, but undergoes no positional changes.

NL, rhythm in a night-light eye, the pigment moving into a typical dark position.

DD, rhythm in a day-dark eye, the pigment moving into the position characteristic for a light-adapted retina.

such differences in response may possibly be due to threshold variations in reactivity to the same hormone, or, there may be two hormones involved, one for the distal pigment and one for the reflecting pigment.

The mechanisms involved in the migration of the retinal pigments in the four brachyurans reported here is less open to analysis chiefly because so little is known about them. These crustaceans are the only ones thus far reported which show a pronounced periodicity in both the distal and in the proximal pigments at the same time. *Cambarus* and *Peneopsis* seem to fall into the same group in that the proximal pigment shows the rhythm.

The mediating agency for the migration of the proximal pigment is not known. In *Palaeomonetes* the eye-stalk extracts which affect the distal and the reflecting pigments have no effect on the migration of the proximal pigment. Early workers on the migration of the proximal retinal pigment were of the view that this activity was under nervous control. But as Bennitt (1932*b*) states, the main argument against this belief is that no efferent nerve fibers have been found supplying these cells, their only nervous connection apparently being afferent fibers going to the optic ganglia (Parker, 1895). From the results of his experiments on the interrelation between the eyes of crustaceans (with regard to proximal pigment migration) Bennitt (1932*b*) believes that an endocrine control may be involved.

It is evident from this discussion that the possibility of formulating a general theory for the phenomenon of persisting diurnal rhythm is still remote. The fact that those crustaceans which have been studied lack the uniformity of behavior that is sought by the experimentalist, is probably sufficient proof of the complexity of the mechanism. In our present state of knowledge it can only be hoped that when the retinal pigments of other crustaceans have been studied with regard to hormonal control as in *Palaeomonetes*, and the innervation of the proximal pigment cells studied by means of modern neurological techniques, a sufficient amount of information will have been gathered to attempt a general explanation of persistent periodicity in the retinal pigment migration of crustaceans.

#### SUMMARY

1. Persistence of a diurnal rhythm in the migration of the retinal pigments of several Bermudan crustaceans, in spite of constant conditions of illumination or of darkness, is reported. Two macrurans, a new species of *Eusicyonia* and *Trachypneopsis mobilispinis*, show the distal retinal pigment in the position characteristic for the dark-adapted eye when the retinas of illuminated specimens are fixed at night.

2. Four species of brachyurans, *Portunus anceps*, *P. depressifrons*, *Parthenope serrata*, and *Calappa flammea*, show the distal and the proximal pigments in the typical light-adapted position when the specimens are kept in the dark-room and are fixed during the day.

3. The retinas of some of the macrurans showed deficiencies or absence of the reflecting pigment. This is thought to be due to differences in metabolism rather than to fixation artifacts.

4. Hormones are considered as the possible mediating agency involved in the phenomenon of persisting diurnal retinal rhythms.

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